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ORIGINAL PAPER

# Non-native fishes in Brazilian freshwaters: identifying biases and gaps in ecological research

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**Abstract** Brazil is the country in the world with the highest freshwater fish diversity. Because of the high rates of species introduction, the number of publications about invasive fish has increased in the last decades in this country. We conducted a systematic review of the literature to identify knowledge patterns and gaps related to the introduction of non-native fishes in distinct Brazilian freshwater ecosystems. Compared to the last official report, we found that the number of records in the literature is three times greater, with at least 352 non-native freshwater fish species (255 translocated and 97 exotics). Studies were concentrated in developed and impacted regions of the country and were mostly conducted in reservoirs and rivers. Only 7% of the studies tested invasion hypotheses, mainly those in the so-called Darwin's and trait concept clusters. Studies that assessed the effects of non-native species investigated a few species, such as *Oreochromis niloticus*, *Coptodon rendalli*, or *Cichla kelberi*. However, the impacts of most species, especially those translocated among Brazilian ecoregions, remain largely unexplored. Therefore, the fish invasion literature in Brazil still has relevant knowledge gaps, biases, and research topics needing investigation. This picture prevents a proper understanding of the ecological and socio-economic consequences of fish introductions to native ecosystems, especially in highly biodiverse regions such as the Amazon. Future research and government agendas should fill these knowledge gaps to allow the establishment of effective surveillance, control, and management programs for non-native fishes in Brazilian freshwaters.

**Keywords** Introduced fishes · Review · Invasion hypotheses · Ecological impacts · Translocated species

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## Introduction

Invasive non-native species are one of the major components of human-mediated global change (Ricciardi 2007; Simberloff et al. 2013). Freshwater ecosystems are among the environments most affected by species invasions and their impacts due to long histories of introductions and hydrologic alteration, among other factors (García-Berthou et al. 2005; Casal 2006; Ricciardi and MacIsaac 2011; Albert et al. 2021). Despite representing a small fraction of the Earth's surface, these environments harbor about 12% of all described species in the world (i.e., more than 140,000) and provide crucial economic and well-being benefits to humans (Reid et al. 2019; Albert et al. 2021). Among aquatic organisms, freshwater fish are one of the most introduced and threatened groups (Gozlan et al. 2010; Olden et al. 2010). Due to the growth in global trade and human mobility, fishes have been widely introduced outside their native range for different purposes (e.g., aquaculture and recreational fishing) (Cambray 2003). Introduced fishes often cause ecological changes in invaded ecosystems, potentially leading to the extinction of native or endemic species and accelerating biotic homogenization (Rahel 2002; Clavero and García-Berthou 2005). Consequently, fish invasions in freshwater systems have become a frequent research topic of ecologists and conservation biologists (MacIsaac et al. 2011; Ricciardi and MacIsaac 2011; Boltovskoy et al. 2018).

One of the most fundamental questions in invasion biology is what ecological factors drive the establishment of introduced species in recipient ecosystems (Catford et al. 2009). Understanding the establishment process helps predict new potential introductions and prevent future invasions, advances ecological and evolutionary theory, and is a key tool for management decisions (Cucherousset and Olden 2011). Several invasion hypotheses try to explain invasion success (Catford et al. 2009; Chabrerie et al. 2019; Enders et al. 2020). In a recent synthesis, these hypotheses were classified into five concept clusters according to particular perspectives on biological invasions (Enders et al. 2020): (1) biotic interaction, (2) Darwin's cluster, (3) trait, (4) propagule, and (5) resource availability clusters. The biotic interaction cluster includes hypotheses that consider the role of interspecific interactions (most them negative) on invasion success. Darwin's cluster considers species' evolutionary legacies, mainly emphasizing the importance of niche similarity between native and invasive species. The trait cluster highlights the importance of species traits to invasion success. The propagule cluster relates establishment success to the number and frequency of introduced individuals. Finally, the resource availability cluster includes hypotheses that associate invasion success with access to resources in the new environment (Enders et al. 2020). Studies have reported the contribution of different ecological mechanisms proposed by these clusters for fish invasion (Marchetti et al. 2004; Queiroz-Sousa et al. 2018; Chabrerie et al. 2019). However, their relative importance is context-dependent and varies with species characteristics and recipient ecosystems (Catford et al. 2009; Rocha and Cianciaruso 2021). Moreover, there is no synthesis of how these hypotheses have been explored in tropical freshwater systems.

The ecological impacts of non-native species are another critical question in invasion ecology (Boltovskoy et al. 2018) because it is especially relevant for developing and prioritizing mitigation and management programs (Cucherousset and Olden 2011). Fish invasions can directly or indirectly affect a range of components in freshwater ecosystems (Cucherousset and Olden 2011). For example, they can lead to species extinction or changes in food webs due to harmful interactions (i.e., predation, competition, hybridization, or parasitism) with fishes or other native organisms (Gozlan et al. 2010). Invasive fishes may also affect environmental conditions and ecosystem functions. For instance, the widely introduced common carp (*Cyprinus carpio*) increases nutrient concentration in the water column due to bioturbation, affecting nutrient cycling (Matsuzaki et al. 2009). Vilà et al. (2010) found that introductions of brook trout (*Salvelinus fontinalis*) impact ecosystem services in European freshwaters by affecting recreational use through declines of native salmonids and modifying water quality through changes in nutrient cycling. Capps and Flecker (2013) also found alterations in nutrient cycling caused by the invasion of a catfish (*Pterygoplichthys* sp.) in a nutrient-limited stream.

Several fish species have been repeatedly introduced to different regions of the world and research efforts about invasion impacts have increased over time (Gherardi 2007b; Gozlan 2008; MacIsaac et al. 2011). However, researchers tend to concentrate on a few non-native fish species (Cucherousset and Olden 2011; Crystal-Ornelas and Lockwood 2020). Many factors can explain this pattern. For instance, salmonid species (e.g., rainbow trout, *Oncorhynchus mykiss*) receive more attention due to their commercial value and popularity (Gherardi 2007a; Zenni et al. 2021). Similarly, non-native fishes with well-recognized detrimental impacts, such as the common carp, have had their ecological effects studied for different ecosystems (MacIsaac et al. 2011). Widely introduced species also receive more attention. For instance, mosquitofishes (*Gambusia affinis* and *G. holbrooki*) have been successfully introduced into many countries and are easily found in freshwater ecosystems (Welcomme 1988; García-Berthou et al. 2005). However, the fact that the vast majority of non-native species were not studied does not mean a lack of ecological impacts (Gherardi 2007a; Simberloff et al. 2013). Therefore, identifying general patterns related to the frequency and context to which non-native fish species impacts have been studied in Brazilian freshwater ecosystems allow us to identify knowledge gaps and future research needs.

Brazil is the country in the world with the highest freshwater fish diversity, with around 3300 species, most of which are native or endemic to specific freshwater systems or ecoregions (Reis et al. 2003; Agostinho et al. 2005). For example, in the Iguassu ecoregion, there are 100 described fish species, approximately 70% considered endemic (Agostinho et al. 2005; Daga et al. 2016). According to the last report from the Brazilian Environmental Ministry (Latini et al. 2016) there are 109 non-native fish species occurring in Brazil. Of these, 54 are translocated (species native to Brazil translocated outside their natural range within Brazil) and 55 are exotic (species introduced in Brazil). These introductions are mainly related to human activities such as fish stocking, aquaculture, the aquarium trade, and recreational fishing (Britton and Orsi 2012; Ortega et al. 2015; Latini et al. 2016; Garcia et al. 2018; Gubiani et al. 2018). Combined with these human activities, current national policies foster unsustainable practices that increase introduction rates and the spread of non-native fishes in different Brazilian freshwater systems and ecoregions (Pelicice et al. 2017). For example, plans to massively expand aquaculture in natural water bodies are especially concerning because they often involve non-native fishes that cause negative impacts on receptor ecosystems (Vitule et al. 2014; Lima et al. 2018; Charvet et al. 2021). Following the high introduction rates, the number of publications about non-native species in Brazilian freshwater ecosystems has markedly increased in the last decades (Frehse et al. 2016; Gubiani et al. 2018; Pereira et al. 2018).

This study reviews the literature about non-native fish species in Brazilian freshwater ecosystems, identifying biases in the current state of knowledge and scientific gaps in the field. For this, we focused on (1) the number of exotic and translocated species introduced in distinct Brazilian ecosystems; (2) which freshwater ecoregions and systems, research topics, and invasion hypotheses are more addressed in the literature; and (3) which components of recipient ecosystems and type of non-native species are investigated when assessing the impact of invasions.

## Methods

In December 2020, we conducted a systematic review in the Web of Science, Scopus, and Scielo databases and literature used by previous reviews (Daga et al. 2016; Frehse, et al. 2016; Latini et al. 2016; Pereira et al. 2018; Ruaro et al. 2020), searching for all publications about non-native freshwater fishes in Brazil. We conducted the study following the PRISMA protocol for systematic reviews (Moher et al. 2009). The following keywords were included in the search string of the databases: topic = (fish* OR (scientific name of all non-native freshwater fishes reported as occurring in Brazilian freshwaters separated by the Boolean operator 'OR')) AND topic = (inva* OR alien OR exotic OR non-native OR non-indigenous OR introduced) AND topic = (aquatic OR freshwater OR reservoir OR lake OR stream OR river OR lagoon OR floodplain OR wetland) AND all research fields = (Brazil). The term "Brazil" was included in the ''all research fields'' to include studies conducted in Brazil without mentioning this keyword in the topic. The timespan considered was all years up to the date of the search. Then, we refined the search looking for articles and reviews using the "area" filter for "Environmental Sciences", "Ecology", "Zoology", "Freshwater Biology", "Biodiversity", "Conservation", "Fisheries" and "Water Resources".

The term "non-native" is commonly used to define a species introduced to areas beyond its native range (Kolar and Lodge 2001; Xiong et al. 2015; Daga et al. 2016). Therefore, we considered non-native species those (1) native to Brazil but translocated outside their natural range within Brazil (translocated); (2) introduced into Brazil from other countries or regions (hereafter, exotic species). In our search, we included the 109 scientific names of non-native fishes (i.e., translocated and exotics) occurring in Brazilian freshwaters according to the last Brazilian Environmental Ministry report (Latini et al. 2016).

We established two criteria for a study to be included in our review: (1) the article assessed the ecology or at least mentioned the occurrence of a fish species as non-native, and (2) the study was conducted in a Brazilian freshwater ecosystem. There was no language restriction in the search. We excluded studies carried out in estuaries or coastal lagoons because these are transitional ecosystems with saline environments and non-native marine fishes. To update the last official report of non-native fish species in Brazilian freshwaters (Latini et al. 2016), we recorded all non-native species names in studies published after 2015 (including Bueno et al. 2021 and Tonella et al. 2022). Then, we classified these species as translocated or exotic according to FishBase (Froese and Pauly 2021). We also registered the estimated introduction year in Brazilian freshwaters for each species. For this, we did an exhaustive search in the literature. When the introduction year was not found, we considered the oldest sampling date reporting the occurrence of the species in the literature or the oldest species occurrence record available in the Brazilian Biodiversity Information Facility Repository (SiBBr; http://www.sibbr.gov.br). Species names followed the list of valid species names in Eschmeyer's Catalog of Fishes (Fricke et al. 2021). For all selected articles, we collected information about the freshwater ecoregion, the type of freshwater system, and the research topic studied. We identified the ecoregions following Abell et al. (2008) and considered the following freshwater system types: floodplain, lagoon, lake, reservoir, river, and stream.

We classified research topics addressed in the studies into biology/genetics/ecology (BGE), occurrence, impact, introduction vectors, invasion hypotheses, policy/management, and reviews. The BGE topic included articles that investigated biology (e.g., diet and reproduction), genetic aspects, or basic ecological questions (for example, the influence of environmental factors on temporal or spatial dynamics of species) of non-native fishes. The occurrence topic consisted of articles reporting new non-native species or records, while the impact topic covered studies that assessed the effects or discussed potential impacts of non-native fishes. In the introduction vectors topic, we included studies examining introduction vectors associated with non-native species occurrence. For the invasion hypotheses, we considered studies assessing hypotheses related to fish invasion success in freshwater systems. Finally, policy/management studies were those related to public policy (legislation) or conservation management (e.g., mitigation programs) for non-native fishes in Brazilian freshwater ecosystems.

For those articles concerning invasion hypotheses, we identified the hypothesis and its respective concept cluster following Enders et al. (2020). The five concept clusters considered were: biotic interactions, Darwin's, trait, propagule, and resource availability. For those papers evaluating the impact of non-native fishes, we also checked if the effect focused on: native fishes, other native organisms, ecosystem effects (ecosystem functions and habitat conditions), and socioeconomic interests. We also determined if the study evaluated the impact of either a specific or a set of non-native species (i.e., a general effect) on ecosystem components; for studies assessing the effects of specific fish species, we compiled the scientific name of the species. We conducted multiple counts per article when needed; some studies, for example, have been conducted in more than one ecoregion or more than one freshwater system. For review articles, we only collated information on the research topic studied. Therefore, the results reflect the proportion of the total articles selected for this review, and the sum of the proportions of categories can reach values greater than 100%.

## Results

Our search resulted in 1666 articles, of which 390 matched the selection criteria and constituted the final list for this systematic review (see Appendices 1 and 2 and Fig. S1 in Electronic Supplementary Material). We found 243 new non-native fish species records in the literature besides the 109 already listed in the last official report. Therefore, we are now aware of 352 non-native species occurring in Brazilian freshwaters, of which 255 are translocated species and 97 are exotic (Table S1). We were able to estimate the introduction year for 342 species (Table S1). The first records of species introductions are the translocated *Satanoperca jurupari*, *Duopalatinus emarginatus*,

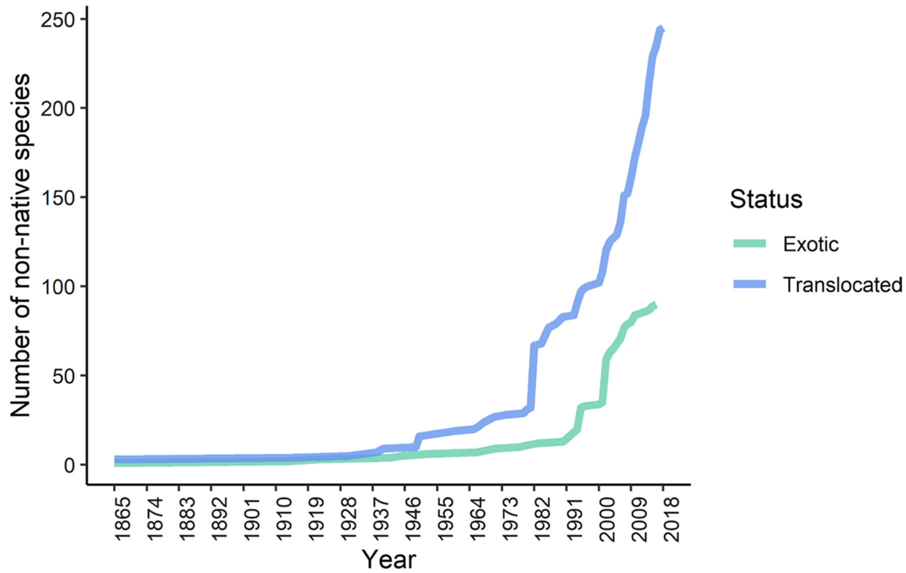


**Fig. 1** Cumulative number of introductions of non-native species (exotic and translocated) over time in Brazilian freshwaters

*Phalloceros caudimaculatus*, and the exotic cascarudo (*Callichthys callichthys*), all in 1865. The number of translocated species greatly increased in the 1980's and, since then, has been increasing at a fast pace. The number of exotic introductions started to increase in the 1990's and continues to increase, even if in lower numbers when compared to translocated species (Fig. 1). Most studies were conducted in the Upper Parana (54.4%, $n=212$) followed by Paraiba do Sul (10%, $n=38$), Northeastern Mata Atlantica (8.2%, $n=32$) and São Francisco (7.2%, $n=28$) freshwater ecoregions (Fig. 2A). Regarding freshwater systems, studies were mainly conducted in reservoirs (45%, $n=176$), followed by rivers (30%, $n=116$) (Fig. 2B). The most explored research topics in publications were occurrence (43%, $n=168$), BGE (36%, $n=142$), and the impact of non-native species (12.5%, $n=48$). The paucity of studies focusing on other research topics is noteworthy (Fig. 2C).

Although only 7% ($n=27$) of the studies evaluated invasion hypotheses, 13 hypotheses were used to explain fish invasions in Brazil (Table 1). Overall, researchers have mostly explored hypotheses related to Darwin's ($n=20$) and trait ($n=11$) clusters (Table 1). Most articles focused on the "ideal weed hypothesis" ($n=5$), in which invasion success is related to specific fish traits. Most studies about the impact of non-native species assessed their effects on native fishes (10%, $n=38$; Fig. 2D), whereas only a few evaluated their impact on socioeconomic aspects (1%, $n=4$). Generally, these studies focused on a particular non-native species (9%, $n=36$) rather than in species groups (3%, $n=12$, Table S2). Considering all studies that evaluated the impact of specific non-native species, only 47 species were studied (13% of the non-native species occurring in Brazilian freshwaters). Among these species, the most investigated were the exotics Nile tilapia (*Oreochromis niloticus*) and redbreast tilapia (*Coptodon rendalli*), representing 2.8% ($n=11$) and 1% ( $n=4$), respectively, and the translocated yellow peacock bass (*Cichla kelberi*) representing 1.5% ($n=6$) of studies (Figs. 2E and 3).

## Discussion

According to our findings, the number of non-native freshwater fish species occurring in Brazilian freshwaters is three times higher than previously reported (Latini et al. 2016). This result is due to recent checklists and data papers that gathered information about occurrences using data from research groups across distinct ecoregions in Brazil (Daga et al. 2016; Frota et al. 2016, 2019; Dos Reis et al. 2020; Bueno et al. 2021; Tonella et al. 2022). Most non-native species records are due to translocations. The temporal introduction trend for these species began sharply increasing in the 1980s with the Itaipu dam construction in the Upper Parana ecoregion that eliminated the Sete Quedas falls, a major natural barrier in the

**Fig. 2** Percentage of studies selected ($n=390$) according to the **A** freshwater ecoregion considered; **B** ecosystem type; **C** research topic addressed (BGE = biology/genetics/ecology); **D** focus of the impact for studies evaluating the impact of invasion; and **E** species that had the specific impact assessed. The complete list of all species that had their specific impact assessed (47) and the respective number of studies are available in Fig. S1. In **E**, the codes "PSqu.", "GPro.", "CRen.", "CKel.", "ONil." represent the species *Plagioscion squamosissimus, Geophagus proximus, Coptodon rendalli, Cichla kelberi* and *Oreochromis niloticus*, respectively. In all graphs, we also indicate the freshwater ecoregion for each category (color label in (A)); studies that are not specific to a freshwater ecoregion are in magenta

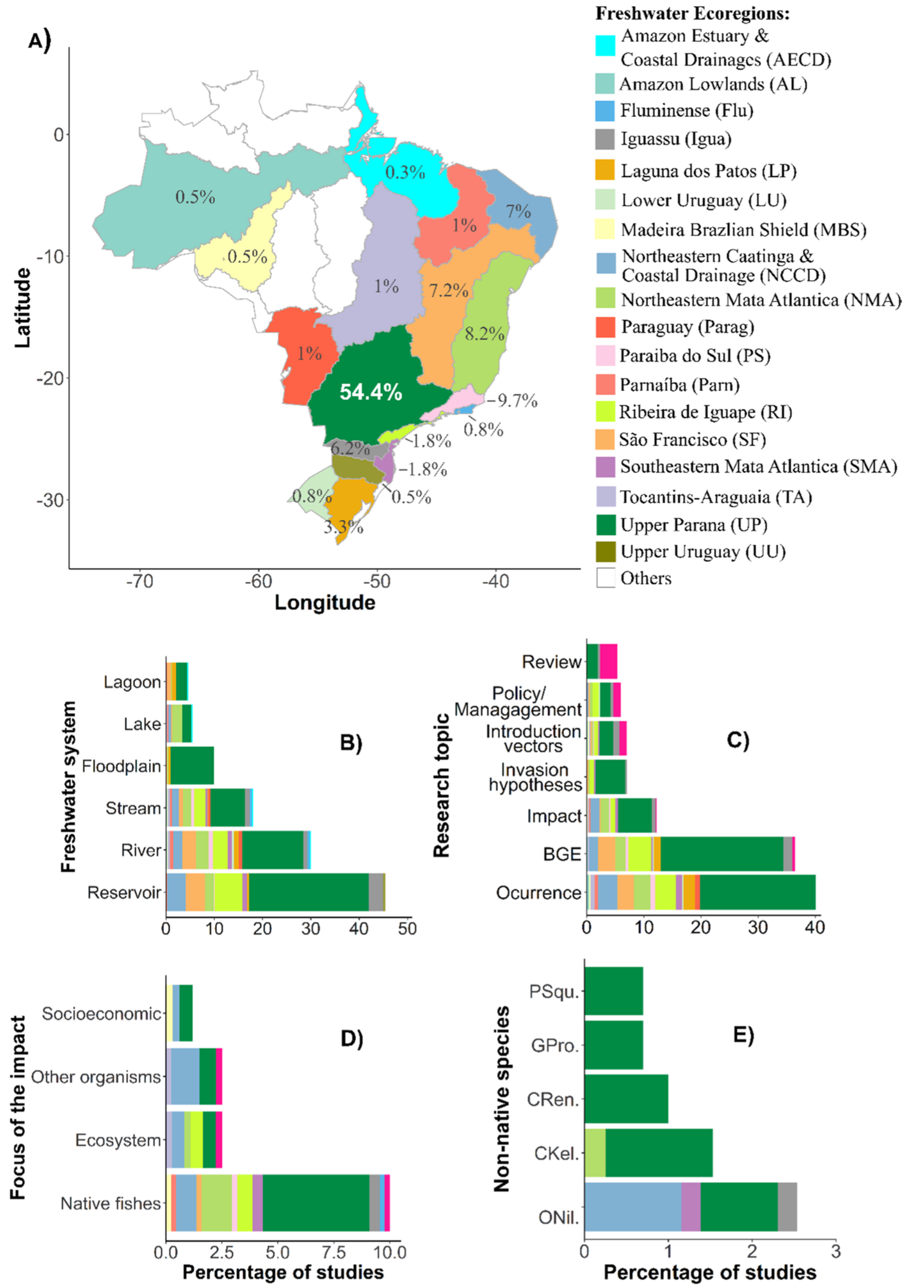

**Table 1** References identified in the literature review that analyze invasion hypotheses (following Enders et al. 2020). We did not identify studies addressing the 26 other hypotheses described by Enders et al. (2020)

| Concept cluster | Invasion hypothesis | Hypothesis description | References |
|---|---|---|---|
| Biotic interaction | Enemy release | The absence of natural enemies in the introduced range explains the establishment success of non-natives (Keane and Crawley 2002) | Lima-Junior et al. (2015) |
| Darwin's Cluster | Biotic Acceptance | Ecosystems accommodate the establishment and coexistence of non-native species despite the presence and abundance of native species (Stohlgren et al. 2006) | Thomaz et al. (2012), dos Santos et al. (2018b, a) |
| | Biotic Resistance | Ecosystems with high diversity are more resistant against non-native species than ecosystems with low diversity (Levine and D'Antonio 1999; Elton 2020) | Thomaz et al. (2012), Ribas et al. (2017), dos Santos et al. (2018b, a) |
| | Darwin's naturalization | Non-native species establishes more in areas that are poor in closely related species than in areas that are rich in closely related species (Darwin 1859) | Skóra et al. (2015) |
| | Limiting similarity | The establishment success of non-native species is high if they differ from native species, and low if they are more similar to native species (MacArthur and Levins 1967) | Pereira et al. (2017) |
| | Ecological "naivety" | The establishment of a non-native species is influenced by the evolutionary history of the invaded community. Largest impacts are caused by species (e.g., predators, herbivores) invading systems where no ecologically similar species exist (Diamond and Case 1986; Ricciardi and Atkinson 2004) | Kovalenko et al. (2010), Pereira et al. (2019) |
| Trait/Darwin's cluster | Adaptation | Establishment success depends on adaptation to conditions in the recipient ecosystem before and/or after introduction. Non-native species more related to native species have more success in adaptation (Duncan and Williams 2002) | Skóra et al. (2015), Pereira et al. (2017) |
| | Habitat filtering | The establishment success of non-native species in the new area is higher if they are pre-adapted to this area (Weiher and Keddy 1995) | Espínola et al. (2010), Agostinho et al. (2015), Gois et al. (2015), Frederico et al. (2019) |
| | Ideal weed | The establishment success of non-native species depends on its specific traits (Baker 1974; Rejmanek and Richardson 1996) | Pereira et al. (2015), Nanini-Costa et al. (2017), Mendonça et al. (2018), Tonella et al. (2018), Garcia et al. (2020) |

**Table 1** (continued)

| Concept cluster | Invasion hypothesis | Hypothesis description | References |
|---|---|---|---|
| Resource availability | Disturbance | Non-native species establishes more in highly disturbed than in relatively undisturbed ecosystems (Elton 1958; Hobbs and Huenneke 1992) | Linde et al. (2008), Santos et al. (2018b, a), Santana Marques et al. (2020) |
| | Opportunity windows | Non-native species establishes if there is availability of empty niches in the introduced range, and the availability of these niches fluctuates in space and time (Johnstone 1986) | Assis et al. (2017) |
| Propagule | Invasional meltdown | The presence of non-native species in an ecosystem facilitates the establishment of other non-native species, increasing their survival likelihood (Simberloff and Von Holle 1999) | Braga et al. (2020) |
| | Propagule pressure | A high propagule pressure increases establishment success (Lockwood et al. 2009) | Carvalho et al. (2014), Frehse et al. (2020), Teixeira et al. (2020), Forneck et al. (2021) |

region (Skóra et al. 2015; Gubiani et al. 2018). Other practices taken to mitigate the impacts of dam construction on fish diversity were also responsible for increasing translocations, e.g., non-native fish stocking in reservoirs and fish ladders built from the 2000's onwards (Júlio Júnior et al. 2009; Ortega et al. 2015). The intense aquaculture activity in the last decades also contributed to the increasing number of translocations. This is because species escape from cages or excavated tanks (ponds) installed near the freshwater systems by different mechanisms, such as floods, cage or tank rupture, and bad practices in the handling of farmed fishes (Orsi and Agostinho 1999; Azevedo-Santos et al. 2011; Ortega et al. 2015).

Moreover, in recent years, new translocated and exotic species have been reported in Brazilian regions other than Upper Parana (Neuhaus et al. 2016; Froehlich et al. 2017; Rodrigues-Filho et al. 2016; Becker et al. 2016). This also includes the Iguassu and the Paraiba do Sul freshwater ecoregions, which host a high number of endemic species and where new translocations for recreational fishing and aquaculture purposes have been recently reported (Daga et al. 2016; Frota et al. 2016; Delariva et al. 2018; Honorio and Martins 2018). Regarding the exotic species, extensive ornamental fish aquaculture in Paraiba do Sul has been one of the leading causes of several exotic species introductions since the beginning of the 2000s (Magalhaes et al. 2002; Honorio and Martins 2018). Some ecoregions are threatened by recent human activities which facilitate new introductions: the São Francisco and Northeastern Caatinga and Coastal Drainage due to the São Francisco River transposition (Ramos et al. 2018); the Tocantins-Araguaia due to aquaculture (Lima et al. 2018) and several ecoregions in the Amazon region due to damming, aquaculture and the aquarium trade (Lees et al. 2016; Doria et al. 2021). These ecoregions are poorly represented in the literature; therefore, little is known about their fish diversity patterns (Frehse et al. 2020; Junqueira et al. 2020; Lima et al. 2021). This is a matter of great concern not only because the number of non-native fishes is probably much higher than what we found, but also because the effects of these invasions on native freshwater ecosystems and species are unknown.

More than half of the studies were conducted in Upper Parana, the wealthiest and most populated ecoregion in Brazil. This is a region with heavily altered landscapes and intense propagule of non-native species due to human activities, such as aquaculture, fisheries, the aquarium trade, and dam construction (Vitule et al. 2012; Magalhães and Jacobi 2013; Garcia et al. 2018; Gubiani et al. 2018). This region has the highest hydroelectric potential in operation in South America and harbors the second-largest hydroelectric power plant in the world (Itaipu). At the same time, this region concentrates a high number

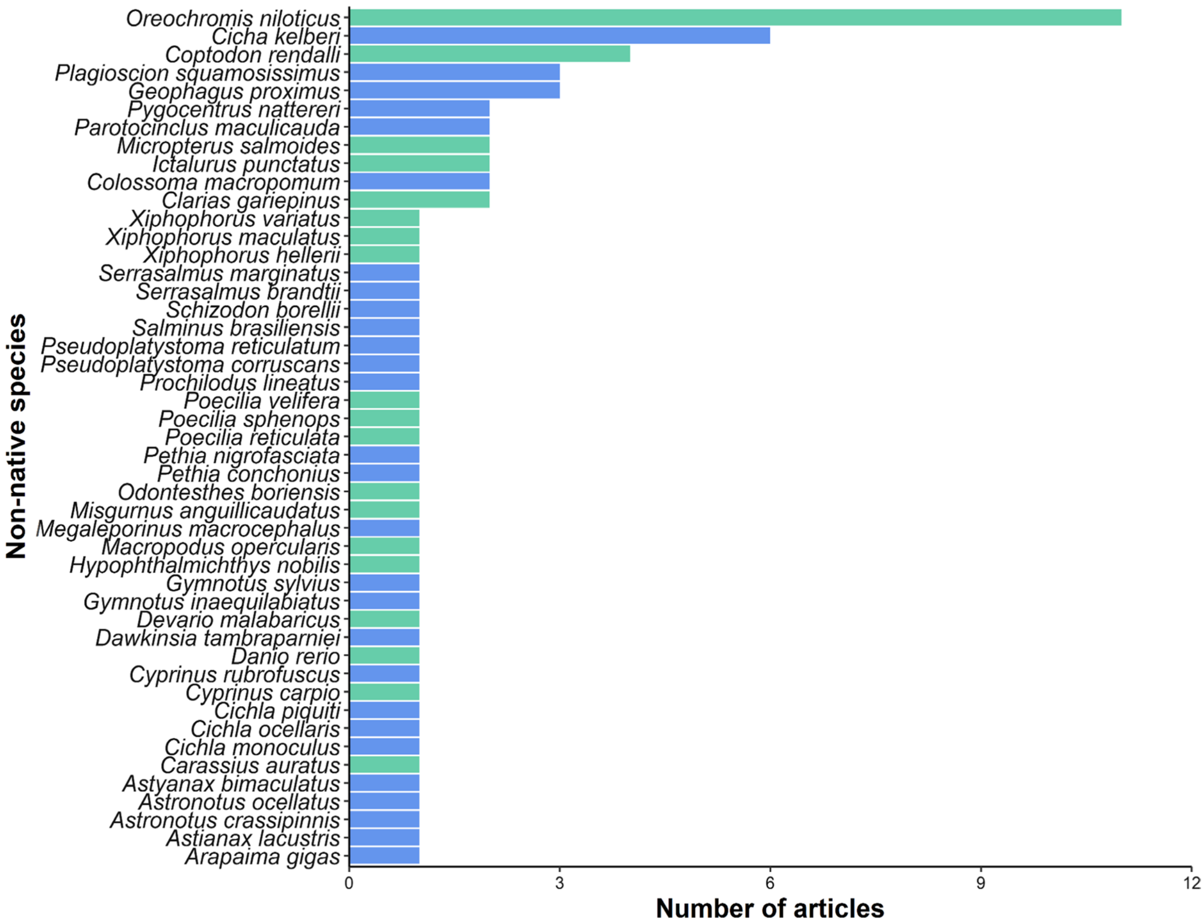


**Fig. 3** Number of articles investigating the ecological impacts of non-native fish species (47 species) classified as exotic (green) or translocated (blue)

of consolidated research groups and programs (e.g., long-term ecological research sites), with one of the highest research budgets in the country (Scarano 2007; Frehse et al. 2016; Ruaro et al. 2020). All this explains the Upper Parana overrepresentation in studies of fish invasion. Most studies (74%) concentrate on a few ecoregions in southern Brazil (Upper Parana, Paraiba do Sul, and Iguassu), where most freshwater systems and research topics were investigated. The underrepresentation of the Tocantins-Araguaia and other ecoregions in the Brazilian Amazon is concerning because of the intense development pressure these regions have faced in recent years. Remarkable examples are the Belo Monte (the third-largest hydroelectric dam in the world) and aquaculture expansion (Lees et al. 2016; Latrubesse et al. 2017; Pelicice et al. 2017). Regarding the importance of these activities as introduction vectors, the scenario of biological invasions is grim for the Amazon.

The high occurrence of non-native fishes in reservoirs and human-impacted rivers also helps to explain why these systems were the most studied. The increased human activities altered the environmental characteristics of these freshwater systems, making them more prone to introductions. Reservoirs are human-made environments where non-native species are introduced for aquaculture, stocking, and recreational fishing (Britton and Orsi 2012; Ortega et al. 2015). Moreover, reservoirs promote the conversion of lotic to lentic environments in the flooded area and downstream, thus altering the hydrologic regime, limnological conditions, and resource availability and favoring the establishment of non-native species more adapted to these new conditions (Poff et al. 2007;

Johnson et al. 2008). Similarly, rivers with more impoundments or water transfers among basins are more susceptible to subsequent invasions, and altered connectivity facilitates the dispersal of these non-native species (Liew et al. 2016; Queiroz-Sousa et al. 2018). For instance, the Paraná River Basin is the second-largest river drainage in the Neotropics and the most impounded with a large number of reservoirs and, consequently, non-native fishes (Agostinho et al. 2008; Vitule et al. 2012; Gubiani et al. 2018). These aspects contribute to the high research effort in the freshwater systems of the Upper Parana ecoregion (Pereira et al. 2018; Frehse et al. 2020). Despite the low number of studies in other aquatic habitats (e.g., lakes and lagoons), as well as other ecoregions, these environments are not free from present and future invasions since new occurrences are increasingly being reported (Rocha and Schiavetti 2007; Harayashiki et al. 2014; Ortega et al. 2015; Froehlich et al. 2017; Larentis et al. 2019; Nobre et al. 2019).

Most studies in Brazilian freshwater ecosystems aim to report new occurrences and update the distribution of non-native fishes. This pattern corroborates that introducing new species is still a current problem since the number of new non-native species reported in recent studies is increasing. These studies also frequently assessed, for example, diet and reproduction (Normando et al. 2009; Vieira et al. 2009; dos Santos et al. 2014; Ganassin et al. 2020), genetic variability or how environmental conditions may affect population and community dynamics of non-native freshwater fish (Casatti et al. 2009; Muniz et al. 2020). Indeed, information about species occurrence and basic ecological and biological aspects of non-native species are crucial to scientists and environmental managers. In contrast, few studies have focused on public policy and fish invasion management, reflecting the necessity to discuss recent unsustainable legislation and assess measures to inspect, control or eradicate harmful non-native fishes in Brazilian water bodies. The lack of reviews considering knowledge produced about non-native freshwater fishes is also noteworthy and must receive attention. Reviews are fundamental to identifying research biases and improving future research agendas (MacIsaac et al. 2011).

The fact that only a few studies tested invasion hypotheses is concerning because many of these theoretical and applied aspects are related to the establishment stage in invasion ecology, which is essential for conceptual understanding and to guide management. The little attention devoted to exploring this topic corroborates a general underrepresentation of aquatic systems (Jeschke et al. 2012), especially in the Neotropics (dos Santos et al. 2018b, a), in the literature on invasion. Nevertheless, considering the few studies we found, all concept clusters of invasion hypotheses have been addressed, with the Darwin's and trait clusters receiving more attention. Therefore, researchers have mainly associated invasion success with an evolutionary perspective emphasizing the importance of non-native species' niches and their similarity with native fishes (e.g., Thomaz et al. 2012; Skóra et al. 2015). However, there is a lack of studies testing hypotheses related to other fundamental aspects of biological invasions such as ecosystem properties (resource availability cluster), interspecific interactions (biotic interactions cluster), and interaction with humans (propagule cluster). This is because hypotheses from these other clusters tend to be tested under controlled environmental conditions, such as field experiments. However, most studies about non-native species in Brazil are observational (Ruaro et al. 2020). For instance, even if the invasional meltdown and propagule pressure hypotheses are well supported for freshwater organisms (Jeschke et al. 2012; Cassey et al. 2018; Rocha and Cianciaruso 2021), they only started to be assessed in Brazilian freshwaters in the last years (Braga et al. 2020; Frehse et al. 2020; Teixeira et al. 2020; Forneck et al. 2021). This is concerning mainly because the current Brazilian environmental policy allows activities that increase propagule pressure and the number of non-native fish species. This includes, for example, the São Francisco River transposition to a river basin in the Northeastern Caatinga and Coastal Drainage and the aquaculture expansion in the Tocantins-Araguaia ecoregion (Lima et al. 2018; Ramos et al. 2018). Therefore, we suggest that future studies should also include manipulative experiments to test hypotheses related to the propagule cluster.

Less than a fifth of the studies we found were designed to evaluate the impacts of non-native fish species on native fauna. Almost all reported negative effects of non-native invasive fishes on native fishes at different biological levels. These include declining population abundances (Pelicice and Agostinho 2009; Kovalenko et al. 2010; Attayde et al. 2011;

Bezerra et al. 2018), loss of taxonomic and functional diversity of native fish communities (Latini and Petrere Jr 2004; Menezes et al. 2012; Queiroz-Sousa et al. 2019), and biotic homogenization (Petesse and Petrere Jr 2012; Vitule et al. 2012). It is interesting to highlight that using functional or evolutionary approaches is a more recent practice (Bezerra et al. 2019; Brito et al. 2020; Daga et al. 2020; Magalhaes et al. 2020). All these impacts can drive native fishes toward local extinction, including endemic species and species with economic potential for humans (Rahel 2002). Nevertheless, there is still a knowledge gap on how fish introductions in Brazil have affected other components of freshwater ecosystems, especially concerning social and economic impacts (but see Hoeinghaus et al. 2009; Attayde et al. 2011). This finding agrees with previous literature reporting that negative impacts on ecosystem services or monetary losses promoted by invasive freshwater fishes are scarcely studied (Gherardi 2007a; Gozlan et al. 2010; Vilà et al. 2010; Crystal-Ornelas and Lockwood 2020). There is also an urgent need to investigate the impacts of fish invasions in poorly-studied ecoregions (for example, the Tocantins-Araguaia and other ecoregions in the Amazon) that are facing a strong expansion of dam construction and aquaculture (Lees et al. 2016; Lima et al. 2018). A comprehensive understanding of the environmental and socioeconomic impacts of these invasions is crucial for developing and implementing effective management measures to prevent, control, or eradicate invasive fishes in these megadiverse ecoregions.

The great effort observed in assessing specific impacts of Nile and redbreast tilapias and the yellow peacock bass can be related to their high occurrence and known invasion impacts. The Nile and redbreast tilapias are native to Africa and widely introduced in Brazil for aquaculture and fisheries purposes (Vasconcelos et al. 2018). The yellow peacock bass is native to the Araguaia and Tocantins basins (Kullander and Ferreira 2006) and is often illegally translocated for recreational fishing and aquaculture in other Brazilian freshwater systems (Pelicice and Agostinho 2009; Ortega et al. 2015). In general, we observed that large-sized species that have fish in their diet (piscivores and omnivores) had received more attention from researchers. This is expected because species with such characteristics are known to negatively impact ecosystems and reduce native species diversity (Canonico et al. 2005). Also, there are current government plans to introduce these species in hydroelectrical reservoirs that threaten native biodiversity in several Brazilian regions (Charvet et al. 2021). However, small-sized species, such as the exotic *Poecilia* spp. introduced in Brazil, are reported as highly harmful because they often carry parasites, eat fish eggs and modify trophic interactions (Arthington 1989; Englund 1999; Rixon et al. 2005). Therefore, we highlight the importance of investigating species with such characteristics.

We emphasize that the impacts of most non-native fishes occurring in Brazilian freshwater ecosystems is still unknown. This is especially true for the translocated species, which compose most non-native fishes in this study. Knowledge gaps about these impacts can result in inappropriate conservation policies and management decisions. To develop practical solutions for reducing species introductions in Brazilian freshwater ecosystems, future studies should evaluate non-native species-specific impacts on ecosystem functioning and the persistence of native species. Also, it is essential to design and implement strategies to mitigate the potential impacts of translocations in all Brazilian freshwater ecoregions. This includes, for example, controlling the population size of these species through intensive and continuous fishing (Santos et al. 2019). There is an urgent need for more studies in ecoregions where introductions are likely to have occurred but were not recorded yet or are occurring due to the expansion of unsustainable activities like aquaculture, river impoundment, and water transfers. Examples of ecoregions that deserve future research efforts are the Tocantins-Araguaia, Northeastern Caatinga and Coastal Drainage, São Francisco, and several other ecoregions in the Brazilian Amazon.

## Competing interests

The authors have not disclosed any competing interests.

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**Data availability** Data used in study is available in Supplementary material.

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